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Cervifurca nasuta n. gen. et sp., an
Interesting Member of the Iniopterygidae
(Subterbranchialia, Chondrichthyes)
from the Pennsylvanian of Indiana, U.S.A.

Rainer Zangerl

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***Cervifurca nasuta* n. gen. et sp., an
Interesting Member of the Iniopterygidae
(Subterbranchialia, Chondrichthyes)
from the Pennsylvanian of Indiana, U.S.A.**

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Cervifurca nasuta n. gen. et sp., an Interesting Member of the Iniopterygidae (Subterbranchialia, Chondrichthyes) from the Pennsylvanian of Indiana, U.S.A.

Rainer Zangerl

Abstract

A new member of the family Iniopterygidae from the Excello Shale (Carbondale Formation, Westphalian lower D, Pennsylvanian) of the Bethel Quarry, southern Pike County, Indiana, is described. This taxon is remarkable for its dorsoventrally flattened body habitus and probably (functionally) correlated enormous size of the pterygopodia, and for orbits that face dorsolaterad. The neurocranium is provided with very prominent nasal capsules, and the pelvic fins consist of a few very short and stout radials. *Cervifurca nasuta* was probably a member of the mobile benthos.

Introduction

During the field seasons of 1982 and 1983 my wife Ann and I, with occasional help from colleagues, students, and friends, quarried the highly fossiliferous Excello Shale at the Field Museum of Natural History's Bethel Church locality in southern Pike County, Indiana. This locality is of particular interest because it contains an abundance of iniopterygians, both species already described (*Iniopteryx rushloui*, *Promexyele peyeri*, *Sibyrhynchus denisoni*, *Iniopera richardsoni*; Zangerl & Case, 1973) and several new taxa. Among the latter is a highly distinctive new member of the family Iniopterygidae, *Cervifurca nasuta*, in which the palatoquadrates are separate cartilages attached to the neurocranium by joints, and the dentition teeth are not fused to form tooth whorls. *Cervifurca nasuta* combines a number of anatomical features suggestive of a benthic habitat for this species.

At the time when E. S. Richardson and I studied the paleoecological aspects of the carbonaceous, sheety black shales (Mecca and Logan Quarry shales; Zangerl & Richardson, 1963), we tacitly assumed that the fishes entombed in these deposits had been regular inhabitants of the ex-

tensive epicontinental marine basin complex (Illinois basin; Forest City basin, etc.) of the north-central United States. There are, however, indications that part of this fish fauna may have entered the epicontinental realm from more distant oceanic waters during repeated transgressions; this applies particularly to the iniopterygians.

Systematic Paleontology

Subclass Subterbranchialia Zangerl, 1979
Order Iniopterygida Zangerl & Case, 1973
Family Iniopterygidae Zangerl & Case, 1973

Cervifurca, gen. nov.

Type Species

Cervifurca nasuta, sp. nov.

Diagnosis

Iniopterygid with dorsoventrally flattened body. Neurocranium in dorsoventral preservation about

as wide as long; orbits facing dorsolaterad; nasal capsules prominently projecting from neurocranium anterolaterally; no or very short rostrum. Well-defined articular facets for attachment of palatoquadrates posterior to orbits. Meckel's cartilage slightly curved, rather sturdy. Ceratohyals about as large as Meckel's cartilages, articulate with triangular basihyal. Fairly large hyoid rays projecting posteroventrad from hyoid elements, probably supporting opercular flaps as in other members of the order.

Dentition teeth, probably 36 in number, relatively very large, consisting of sharp-cusped, probably backward-curved crowns and widely flaring bases; most likely forming single rows of functional teeth on biting edge of each jaw.

Vertebral column consisting of paired neural arch cartilages, declining in height from neck region to tail peduncle, and paired (as preserved) more or less rectangular cartilages, probably located ventrolateral to notochord. Number of vertebral elements approximately 50, exclusive of tail fin.

Scapulocoracoid relatively wide at midlength, strongly curved forward at both ends as in other iniopterygians. A hemispherical joint boss for articulation of basipterygium of pectoral fin occurs a short distance from dorsal end. As in *Iniopteryx rushlaui*, basipterygial region of pectoral fin consisting of relatively large anterior cartilage and much smaller posterior element. Along anterior edge of larger plate is a joint pan for articulation with scapulocoracoid, and along posterior edge a strongly projecting joint knob for articulation with first strongly enlarged fin ray (in males, "rasp"). Rasp with sharp reduction in diameter in distal half, much as in *Promexyele bairdi*, but with relatively small number of hooks, about 18–20 per rasp, with the proximal 7 very much enlarged. About 11 distally very slender radials forming main supports of fin web. At trailing side of fin, four radials proximally fused to form a structure reminiscent of a deer antler. Similar proximal fusion of radials occurs by convergence in *Squatina nactis*, another Carboniferous form of batoid habitus (Lund & Zangerl, 1974). These fused radials and two or three adjacent ones are attached to the smaller basal plate.

Pelvic girdle elements consisting of sturdy cartilages, twice as wide distally as proximally, pierced by three or four foramina (perhaps zonal nerve canals). Distally attached are approximately triangular basipterygial plates of the pelvic "fins," each probably studded with some 25 te-

nacular hooks (in life) consisting of stout, yet acutely pointed, strongly curved crowns and large, bulbous bases. Ten very short and robust radials and two or three slender ones constitute the pelvic fin complex.

Pterygopodia enormously enlarged, consisting of two rhomboidal connecting links, followed by a very long clasper cartilage; the terminal structure, not consisting of calcified cartilage (see below), is about half as long as the preceding clasper element and is provided with three barbs near its end.

Dorsal fin consisting of series of about six fairly sturdy radials.

Etymology

cervus = deer; *furca* = fork.

Cervifurca nasuta, sp. nov.

Diagnosis

Same as for genus.

Etymology

nasutus = (large) nosed.

Holotype

FMNH PF13228 (X-ray [XR]: B83-996) ♂, a partial, slightly disarticulated skeleton lacking the anterior end of the skull (Fig. 1).

HORIZON—Excello Shale (equivalents: black shale over coal IV A, Indiana; black shale over coal IV, Illinois), Carbondale Formation, Desmoines Series, Westphalian lower D, Pennsylvanian.

Locality—Bethel Quarry, excavated during 1982–1983 by Rainer and Ann Zangerl with occasional help from colleagues, friends, and a few devoted amateur collectors. Strip-mine headwall, about center of NW¼ of sec. 3, T3S, R7W (Augusta quadrangle), about 1 km SE of Bethel Church, Pike County, Indiana.

Referred Specimens

HORIZON—Preserved in a fragment of a siderite concretion from a black shale above the Spring-



FIG. 1. *Cervifurca nasuta*, X-ray positive of the plate of the holotype FMNH PF13228 (XR: B83-996); the missing parts of the shoulder girdle and pectoral fin are on the counterplate. The radiograph shows shadows of structures not belonging to *Cervifurca*, such as L, "flag" denticles of *Listracanthus hystrix*; PGR, plaeoniscoid gastric residue mass; PS, a scatter of palaeoniscoid scales; and a background scatter of very large numbers of tiny cladodont denticles that are the topic of a separate account (Zangerl, 1995).

field (no. 5) coal; Carbondale Fm., Desmoines Series, Pennsylvanian. **Locality**—Fulton County, about 20 mi south of Galesburg, Illinois. The label mentions Fred R. Jelliff, Galesburg, Illinois, who may have been the collector. **Specimen**—Univer-

sity of Illinois Museum of Natural History (UIMNH) 11378 (Figs. 2, 3). Part of a three-dimensionally preserved, ♂ specimen, consisting of part of the vertebral column, the pelvic fin complex, parts of both pterygopodia, and the dorsal fin.



FIG. 2. *Cervifurca nasuta*, UIMNH 11378, partial, mostly articulated skeleton preserved in a fragment of a large siderite concretion.

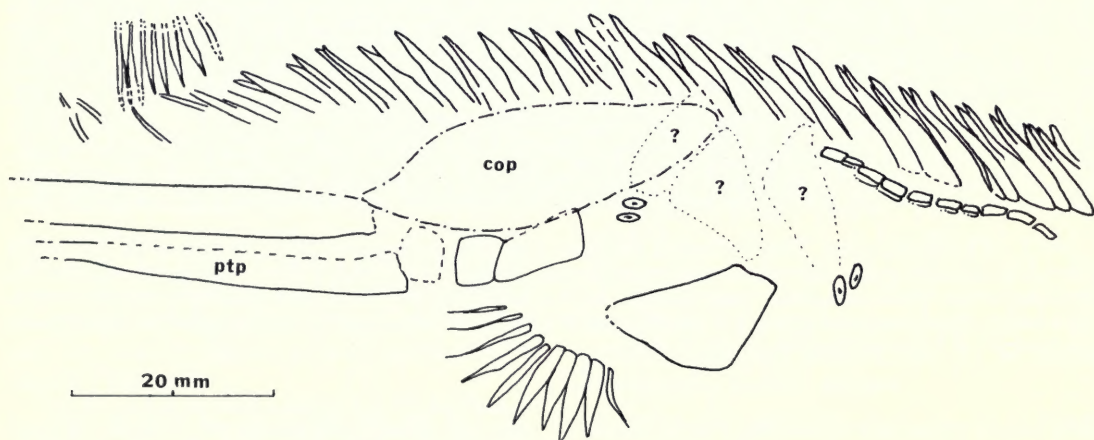


FIG. 3. Drawing of the preserved parts of UIMNH 11378. The pelvic area is somewhat distorted, probably because of the presence of a large coprolitic mass (cop). The question marks indicate very indistinctly outlined cartilages, probably the pelvic cartilages and the basal plate of the pelvic fin of the opposite side. ptp, long elements of the pterygopodia.

HORIZON—Excello Shale (equivalent: black shale over coal IV A, Indiana) Carbondale Fm., Desmoines Series, Westphalian lower D, Pennsylvanian. **Locality**—Barret Cemetery: Strip-mine headwall, NW¼, sec. 3, T3S, R7W (Augusta quadrangle), NW of Barret Cemetery, Pike County, Indiana. **Specimens**—FMNH PF6455 (XR: Barret no. 11), fair ♂ specimen including dorsoventrally preserved braincase and some visceral elements. Collected 1970, by Field Museum party. FMNH PF6456 (XR: Barret no. 7), disarticulated, partial ♂ skeleton. Collected 1970 by Field Museum party.

Locality—Bethel Church: Strip-mine headwall, about center of NW¼ of sec. 3, T3S, R7W (Augusta quadrangle), about 1 km SE of Bethel Church, Pike County, Indiana. **Specimen**—FMNH PF6618 (XR: Bethel no. 51), chewed, disarticulated partial ♂ specimen. Collected 1970 by Field Museum party.

Locality—Bethel Quarry, worked during 1982–1983 at the site of Field Museum of Natural History's Bethel Church locality (see above). **Specimens**—FMNH PF13229 (XR: B83-133C), somewhat disturbed, partial ♂ skeleton. FMNH PF13230 (XR: B83-135), good, partial ♂ skeleton. FMNH PF13231 (B82-384), isolated neurocranium. FMNH PF13232 (XR: B83-483), incompletely recovered ♂ skeleton, partial vertebral column, partial pelvic complex. FMNH PF13233 (XR: B82-240), isolated neurocranium. FMNH PF13234 (XR: B83-510), incompletely recovered ♂ skeleton, partial pectoral fin, partial pterygopodium. FMNH PF13235 (B82-561), isolated neurocranium. FMNH PF13236 (XR: B83-554), mutilated, incomplete skeleton. FMNH PF13237 (XR: B83-136), somewhat disturbed, partial ♂ skeleton. FMNH PF13238 (XR: B83-1039), badly disturbed, partial ♂ skeleton.

HORIZON—Mecca Quarry Shale, black shale over coal III A (Indiana) = Colchester No. 2 (Illinois), Carbondale Fm., Desmoines Series, Westphalian upper C, Pennsylvanian. **Locality**—Chinook Mine, Ayrshire Colliery, south of Staunton, Clay County, Indiana. **Specimen**—FMNH PF5874 (XR: Chinook no. 1), disarticulated, partial ♂ skeleton. Collected by Field Museum party.

REMARKS—All specimens other than UIMNH 11378 show the effects of predation (Zangerl & Richardson, 1963) as well as some bacterial decomposition, the latter affecting especially skeletal elements that had been injured by the predator. The remains preserved in the black, sheety Excello Shale from the Bethel Church and Barret

Cemetery localities are covered with an extremely thin, smooth, and glossy film of pyrite, and hence show excellent surface detail and furnish unusually good X-ray pictures.

It may be noted from the specimen list that all remains (other than the isolated neurocrania, for which the sex cannot be determined) belong to males. Female iniopterygians (of all species) are extremely rare in the present collections, and the one relatively well-preserved female skeleton, FMNH field no. B83-942, from the Bethel Quarry, is a sibyrhynchid probably belonging to an as yet undescribed species.

Description

NEUROCRANIUM AND VISCERAL SKELETON—Three isolated neurocrania, PF13231, PF13233 (Figs. 4, 5), PF13235, and two associated with partial skeletons, PF13236 and PF6455, are all preserved in a dorsoventral burial position. As preserved they resemble somewhat the skull of *Helodus simplex* as depicted by C. Patterson (1965), but closer study shows beyond question that the similarity is superficial: the paired, large openings at midlength of the holostylic neurocranium of *Helodus* are cranioquadrate passages, whereas they are the orbits in the (iniopterygid) autodiastylic (deBeer, 1937, p. 422, Pl. 142) *Cervifurca* skulls.

A better understanding of the *Cervifurca* braincase is gained by comparison with the neurocranium of a modern batoid such as *Raja* where the eyes look out from the dorsal surface of the flattened head. In *Raja* the orbits are delimited by cartilage only medially and anteriorly, where large anterolateral projections enclosing the nasal capsules jut out. This condition is depicted on the right side of Figure 6; on the left side the basic *Raja* pattern is shown as modified in *Cervifurca*, where the orbits are delimited all around by cartilage, and the nasal capsules are in a position comparable to that in *Raja*. In contrast to other iniopterygians, the orbits of *Cervifurca* lack a dorsal cartilage roof, hence the suggestion that the eyes faced dorsolaterad, as in batoids.

Another profound difference between the neurocrania of *Helodus* and *Cervifurca* is the location of articular facets for the visceral skeleton. In the holostylic *Helodus*, joint facets for Meckel's cartilages are located anterior and ventral to the orbits and well forward of the cranioquadrate passages, whereas in *Cervifurca*, the joint facets for



FIG. 4. Isolated neurocranium (plate only) of *Cervifurca nasuta*, PF13233 (B82-240) in dorsoventral burial position; X-ray enlargement. The diagonal shadow across the right orbit is a thickness boundary of the shale slab. The irregular black areas are cartilage pieces that have broken loose from the counterplate. Extraneous shadows in the background belong to palaeoniscoid scales and tiny cladodontid denticles (see note with Fig. 1). X-ray courtesy of John D. Knight, Rockville, Indiana.

the palatoquadrates are situated behind the orbits and lateral to the otic capsules (Figs. 5c,d).

The dorsoventrally preserved neurocrania described above (Figs. 4, 5) are clearly flattened into a near two-dimensional state. In Figure 7 I have tried to visualize, in principle, the original form of the braincase (using modern batoid neurocrania for comparison) as depicted in three cross sections: across the antorbital region, across the orbits, and across the postorbital region. The cross sections, which are, of course, hypothetical, also

indicate the presumed relationship of the palatoquadrates to the neurocranium. In Figure 7B the orbits face dorsad and slightly laterad.

The visceral skeleton is incompletely preserved in all specimens. A palatoquadrate could be tentatively identified only in PF13236 (Fig. 8), where a cartilage of the right size and believable outline lies next to the braincase and close to a Meckel's cartilage. The outline of this element on the X-ray film is obscured both fore and aft by skeletal debris, and its overall form cannot be determined

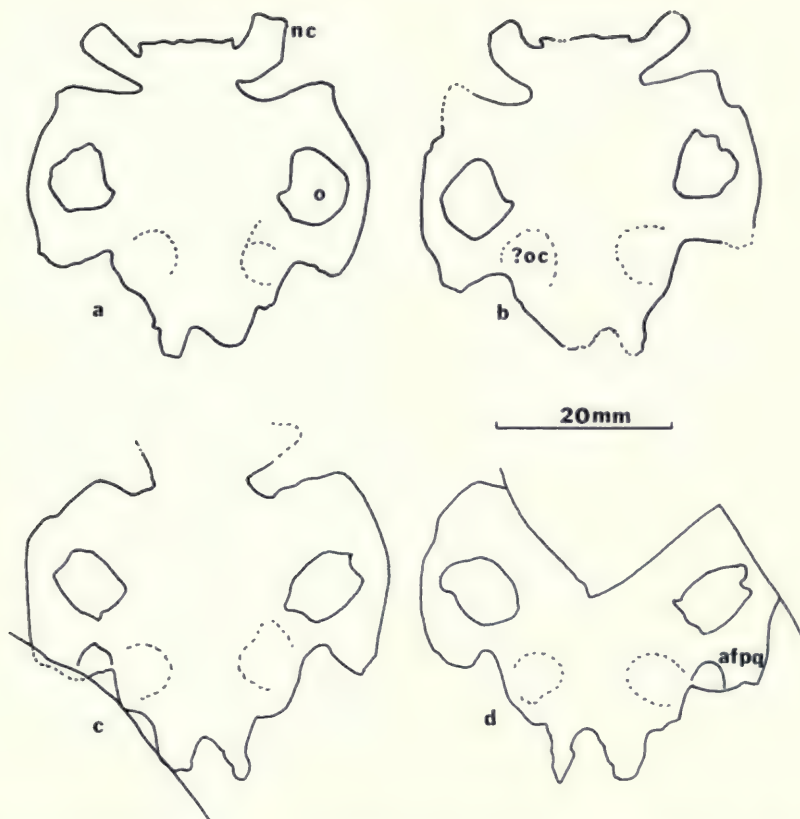


FIG. 5. Neurocranial outlines of *Cervifurca nasuta*, dorsoventral burial position. **a, b**, Plate and counterplate of PF13233 (B82-240), see Fig. 4; **c, d**, plate and counterplate of PF13235 (B82-561). Drawings made from the specimens with the drawing tube of a Wild binocular microscope. afpq, articular facet for the palatoquadrate; nc, nasal capsule; o, orbit; ?oc, otic capsule.

satisfactorily. The outline of the palatoquadrate in the lateral view of the skull (Fig. 7) is a hypothetical interpretation of what the element described above might have looked like.

Meckel's cartilages are present in PF6455 (Fig. 13), PF13229, PF13230 (Fig. 9), and PF13236. They are elements of simple form, slightly S-shaped in dorsoventral aspect; concave articular facets are visible at the posterior ends (Fig. 13). Anteriorly, several specimens show on X-ray film indications of surfaces that probably represent the symphyseal contacts of right and left elements.

DENTITION—As may be gathered from the description of the condition of preservation of the jaws, the dentition teeth are not located in situ with the jaws in any of the specimens. Nevertheless, some assumptions concerning the dentition can be made with some confidence.

The dentition of *Cervifurca nasuta* consists of a number of relatively large functional teeth (Figs.

11f–j), presumably arranged in single rows along the crests of the jaws. Smaller teeth (Figs. 11k–q) of similar morphology, but less than half the size, are intermingled with the larger teeth, and probably represent posterior teeth. In addition, there are minute teeth (faintly visible on radiographs) that most likely are mucous membrane denticles (Fig. 12). A total of 35 large and smaller teeth are preserved in PF13230 (Fig. 9); in PF6455 there are about 34 teeth. If all of these had been functional at the time of death, the dentition would have consisted of eight or nine teeth along the biting edge of each jaw quadrant, an assumption depicted in Figure 7C.

The dentition teeth (Figs. 11f–q) are single cusped and provided with extraordinarily large bases. The crowns consist of dentine, probably orthodentine (to judge from its appearance on broken cusps), surrounding open pulp cavities. A superficial layer of vitrodentine was not observed

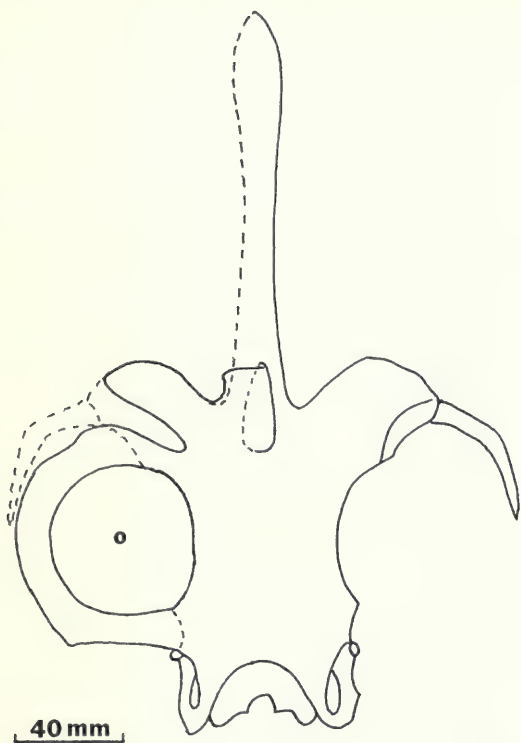


FIG. 6. Outline of the skull of *Raja*, after Gegenbaur (1872, Pl. 13, Fig. 1). The left half of the outline is modified to reflect the condition in *Cervifurca*. o, orbit.

and may have been dissolved after burial. The crown cusps are acutely pointed and curved (presumably backward) and are of differing lengths, probably depending on their position on the jaw. The crowns sit on top of asymmetrically conical bases (Figs. 11k–q), which are strongly flaring. In (presumably) older but not much larger individuals, the bases of these teeth are enormously expanded in the form of fingerlike projections, so that their diameters may reach as much as eight times the largest diameters of the crowns.

None of the specimens show mouth plates (= aggregations of basally fused mucous membrane denticles) homologous to those in *Promexylele* and the sibirhynchids; the lining of the mouth cavity may, however, have been studded with tiny denticles, present in large numbers in front of the head region of PF13229. These very small denticles (200–400 μm base diameter) have bases of oval or irregular outline and low, stout crowns (Fig. 12).

HYOID ARCH AND BRANCHIALIA—These structures have not yet been described for the Iniop-

terygidae; the little that is known pertains to species of the Sibirhynchidae. Cartilages of the hyoid arch and the branchial basket are seen in several specimens of *Cervifurca*, but they are not in articulation and are frequently obscured on X-ray pictures by parts of the neurocranium, the scapulocoracoids, and other elements. In PF6455, however, some parts of this complex lie behind the two lower jaws, and in front of the nasal projections on the neurocranium (Fig. 13). An unpaired triangular element has joint facets at the posterolateral corners, but none in front. This clearly unpaired element may thus be the basihyal. To either side and behind it are elongated cartilages of about the same size as the lower jaws; they have joint facets in front and taper almost to points at the opposite ends. The left one in Figure 13 is almost in articulation with the triangular cartilage identified as the basihyal. The position of these cartilages in this specimen suggests that they articulated in life with the unpaired element between them, and thus represent the ceratohyals. If this interpretation is correct, both the basihyal and the ceratohyals differ considerably in form from those of the Sibirhynchidae (see Zangerl & Case, 1973, Figs. 46, 72, 73; Zangerl, 1981, Fig. 30). The absence of posterodorsal joint facets on the presumed ceratohyals may indicate the lack of calcification at those ends. Behind these probable hyoid elements are a number of very narrow strips of cartilage that are perhaps ceratobranchials (Fig. 13). These are pointed at both ends, which may indicate that some uncalcified cartilage was associated with them. A search for basibranchial elements among the present specimens was negative.

Since the original description of members of the order Iniopterygida (Zangerl & Case, 1973) several specimens have come to light that show beyond question that the scapulocoracoids not only extend far forward ventrally, but actually articulate by means of ball-and-socket joints with what I assume to have been the posteriormost basibranchials (Zangerl, 1981, Fig. 30). None of the *Cervifurca* specimens show this connection, but the ventral, forward-reaching end of the scapulocoracoid is very much elongated and probably had the same relationship to the last basibranchial as in *Sibirhynchus*.

The morphology of the ventral visceral arch elements, as presently understood, is illustrated for *Cervifurca* in Figure 14. Hyoid rays that probably supported opercular flaps, as in extant chimaeroids, are seen in several specimens, for example,

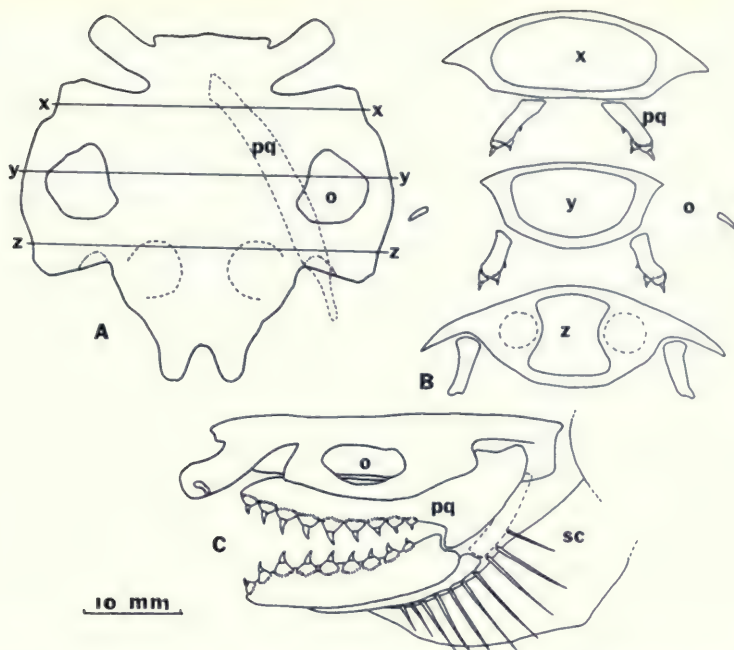


FIG. 7. A, Outline of neurocranium of *Cervifurca nasuta* in dorsoventral burial position. B, Position of hypothetical sections x, y, and z. C, Attempt at reconstruction of the skull in lateral view. The form of the palatoquadrate is almost entirely conjectural. o, orbit; pq, palatoquadrate; sc, scapulocoracoid.

PF13230 (Fig. 10) and PF13237. They are fairly sturdy—a little more than 1 mm in width as preserved—and there appear to be about nine rays on each side.

VERTEBRAL COLUMN—The vertebral column is most completely preserved in the holotype, PF13228, but it is not entirely intact (Figs. 1, 15). It consists of paired neural arches and paired ventral cartilage pieces that may have formed within the notochordal territory, or ventrolateral to it in the notochordal sheath.

The precise number of vertebrae cannot be determined, but a fairly close estimate is possible, as follows: there are about 18 prepelvic vertebrae, of which the anteriormost 6 may be cervical. Of the postpelvic vertebrae, about 14 reach back to the dorsal fin; another 10 or more may have formed the tail peduncle. The total number of vertebrae (minus those supporting the tail fin) may have been around 50.

The cervical vertebrae differ from those farther back in that the neural arch pieces are longer, have enlarged ventral ends, and the neural arches show, in lateral aspect, bulges and constrictions (Fig. 15). The subrectangular ventral cartilages are longer than those farther back, indicating that these

vertebrae were longer as well as taller than the thoracic ones. Behind the cervical series the neural arches gradually diminish in height and the individual arch pieces are of very simple form, widest ventrally and tapering to a point dorsally. This region of the column is preserved in the concretion specimen UIMNH 11378 (Figs. 2, 3), and this specimen shows the right and left neural arch elements almost in perfect preburial configuration—only the slightly diverging dorsal tips show that these cartilages are paired.

SHOULDER GIRDLE AND PECTORAL FIN—As in all other iniopterygians the shoulder girdle cartilages differ from the scapulocoracoids of elasmobranchs where the right and left coracoidal portions meet in a midventral symphysis; in the iniopterygians the ventral halves of the shoulder girdle cartilages are strongly projected forward (Zangerl & Case, 1973, Fig. 36) and end in joint pans that articulate with paired joint bosses on the second basibranchial element (e.g., in *Sibyrhynchus*, Zangerl, 1981, Fig. 30).

None of the shoulder girdle cartilages in any of the available specimens of *Cervifurca* is preserved in its entirety and without injury; hence no detailed description of this structure can be given.



FIG. 8. Radiograph tracings of plate and counterplate of *Cervifurca nasuta*, PF13236 (XR: B83-554). bc, basal cartilage of pectoral fin; Mc, Meckel's cartilage; o, orbit; pe, pelvic element; ?pq, very probably the palatoquadrate—its outline fore and aft is not well defined; sc, scapulocoracoid; tep, terminal element of the pterygopodium.

The shoulder girdle cartilage is rather wide at midlength, and in PF13228 one of them is preserved in articulation with the basal cartilage of the pectoral fin (Fig. 1). In all iniopterygians the joint boss is located on the posterolateral edge of the dorsal half of the scapulocoracoid and articulates with the joint pan on the anteromedial side of the basal cartilage of the pectoral fin.

The basal cartilage bears a pronounced joint boss at its anterolateral corner; this prominent boss articulates by means of a well-developed joint pan on the much enlarged first fin ray, the rasp, of the pectoral fin of the males (Fig. 16). Behind the joint boss the lateral edge of the basal cartilage is irregularly concave and shows attachment facets for about eight fin rays. As in *Iniopteryx rushlaui*, where the last four pectoral radials are attached to a small second basal cartilage (Zangerl & Case, 1973, Fig. 22), there is a second basal cartilage in *Cervifurca* that bears three ra-

dials and the "antler" complex at the trailing side of the fin (Figs. 1, 16B).

The pectoral fin web is relatively large, being supported, in males, by an enlarged first radial (rasp), about 11 fairly slender radials, and the "antler" complex (Figs. 1, 16B, 21, 22). The ball-and-socket joint between the basal cartilage and the rasp is so prominent that there is the possibility that the rasp was not included in the fin web and may have been capable of independent movement. *Cervifurca* has the most extensive pectoral fin web of all presently known iniopterygians, if the above interpretation of the number of radials is correct.

The rasp is relatively thick in its proximal half, then tapers to a long, slender distal portion (Fig. 16A). Its shape is thus similar to that of the rasp of *Promexyele bairdi* (Zangerl & Case, 1973, Figs. 40, 41), but it differs much from the latter by the form, size, and number of the hooks. In

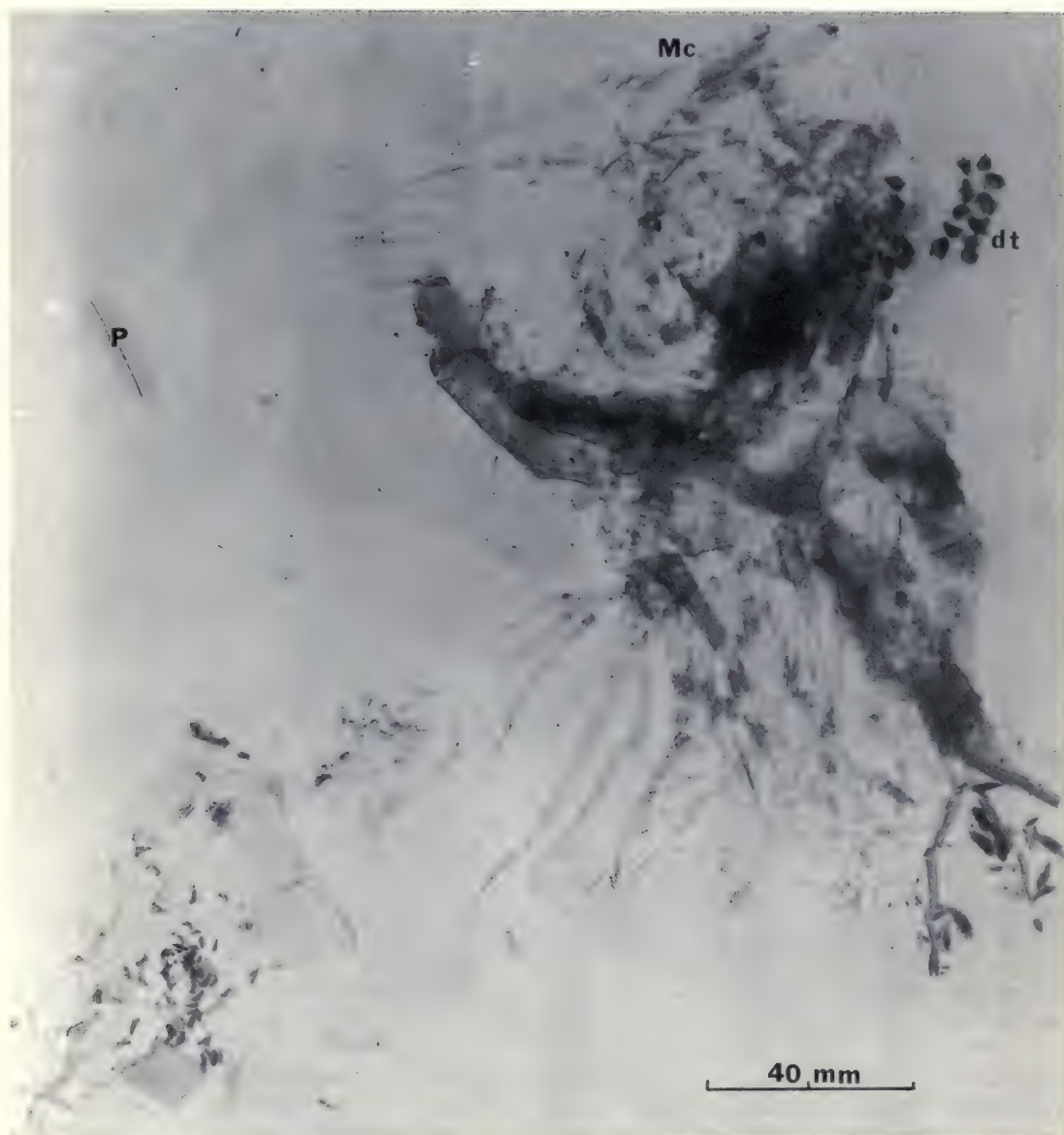


FIG. 9. *Cervifurca nasuta*, PF13230 (XR: B83-135); X-ray positive of plate. This specimen shows a large portion of the dentition but it is not possible to determine to which jaw the longitudinal rows of teeth belong. dt, dentition teeth; Mc, Meckel's cartilage; P, palaeoniscoid element.

Cervifurca, as in *Iniopteryx rushlaui*, there are about 10 hooks in but a single row. The hooks on the proximal half of the rasp are very large (Figs. 11c, 16, 17e-i, 18A-C), and consist of sharply pointed, rather stout crowns and enormously expanded bases that may measure as much as 6 mm in length and 2 mm in width. The total height of these denticles (tip of crown to bottom of base)

may measure more than 2 mm. The bases grew both proximad and distad in the form of finger-shaped projections (Figs. 11c, 17, 18) that fused to form a large platform. Broken crowns of these rasp hooks show a thick layer of dentine (probably orthodentine) surrounding a rather narrow, open pulp cavity (Fig. 18). The base consists of trabecular dentine. The hooks diminish in size



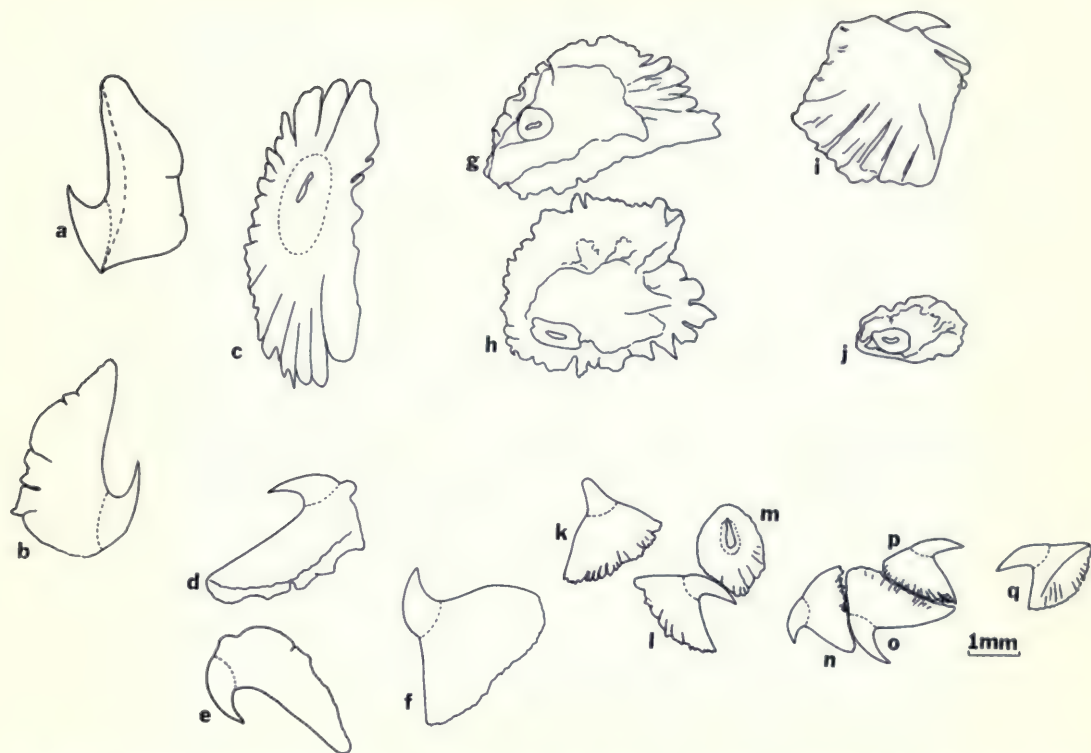


FIG. 11. Outline of dentition teeth, and tenacular and rasp hooks of *Cervifurca nasuta*. a, b, Tenacular hooks; c, large rasp hook of PF13228 (XR: B83-996). d, e, Tenacular hooks; f, dentition tooth of PF13237 (XR: B83-136). g-j, Dentition teeth of PF13230 (XR: B83-135). k-q, dentition teeth of PF13229 (XR: B83-133C). The drawings are tracings from X-ray films, using a Wild binocular microscope drawing tube.

where the rasp cartilage tapers to a thin rod (Fig. 16), and the most distal hooks measure about 1 mm in base length.

PELVIC CARTILAGES, PELVIC FINS, PTERYGOPODIA—The pelvic cartilages of *Cervifurca* have a characteristic shape that is easy to identify on X-ray films (Figs. 1, 16C): a proximal, more or less parallel-sided shaft is distally expanded to about $1\frac{1}{2}$ times the shaft diameter, and where the element expands in width there are several (often four) foramina that may have allowed the passage of zonal nerves and perhaps blood vessels (Fig. 16C).

The pelvic fin of this species is unique among presently known iniopterygians. It consists of a triangular basal cartilage (Fig. 16C) that probably carried a battery of tenacular hooks, and has, along its lateral border, attachment facets for 10

radials, all short and stout except for the first and two slender ones at the posterior end of the fin (Figs. 2, 3, 16C, 21, 22). The radials of this pelvic fin complex are so short and stout that it seems unlikely that they supported a fin membrane, and that the structure as a whole functioned as a fin. It seems possible that the sturdy radials were stiff in life and may have been used for crawling or some other activity not related to swimming.

Ceratotrachia, present in the pelvic fins of *Iniopteryx rushlaui*, could not be found in any specimen of *Cervifurca*, including the concretion specimen UIMNH 11378.

Cervifurca has a large number of tenacular hooks that are highly characteristic in form (Figs. 11, 17, 18, 20, 21). The numbers range from approximately 36 (= 18 pairs in PF13237) to ap-

FIG. 10. *Cervifurca nasuta*, PF13230 (XR: B83-135); X-ray positive of counterplate. This shows the hyoid rays (hr). The skull is badly mutilated.

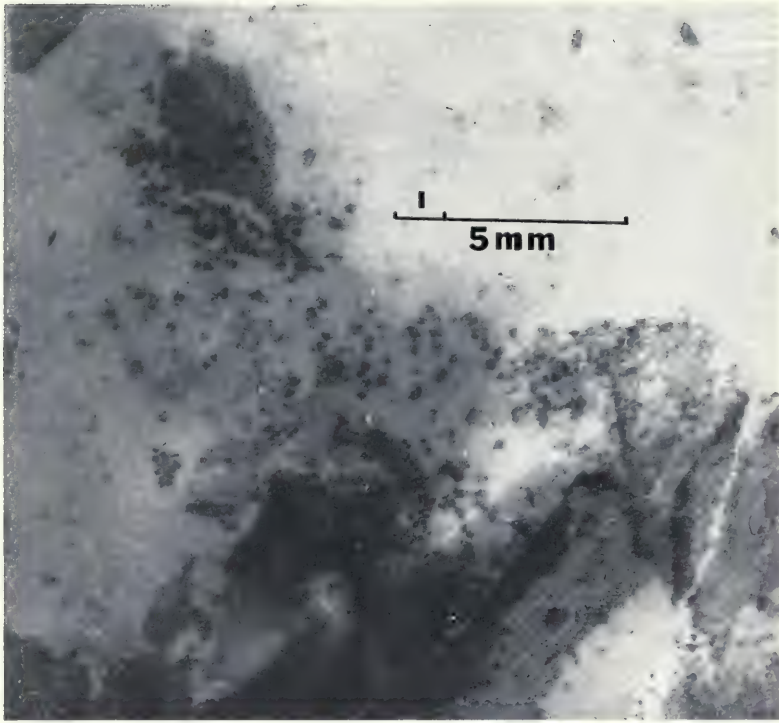


FIG. 12. X-ray positive of anterior end of specimen PF13229 (XR: B83-133C) showing a large number of minute denticles of the general form of the dentition teeth of *Cervifurca nasuta*. They might be mucous membrane denticles of the mouth cavity.

proximately 44 (= 22 pairs in PF13228) to approximately 50 (= 25 pairs in PF13230). The crown of these denticles extends from one end of the base (probably the forward end), and curves (? backward) over the base so that the apex in many cases is above the midlength point of the base (Figs. 11, 17, 18); more rarely the base is elongated and the crown reaches only a short distance over the base. The crowns are circular to slightly oval in cross section and vary somewhat in size relative to the bases (Figs. 17, 18). The base exhibits a number of highly characteristic features. It has lateral and basal bulges and often a rather pronounced ridge that runs clear around the base just below the crown—base junction (Figs. 11, 17, 18). In any given specimen the tenacular hooks tend to be fairly uniform in size, but smaller hooks are present in PF13229 and PF13230 (Figs. 17, 18). I assume that these denticles were borne on the basal cartilages of the pelvic fins because there is no evidence of separate tenacula.

The pterygopodium (Figs. 1–3, 16C, 19–21) is of enormous size relative to the size of the fish.

It is more than three times the length of the neurocranium and consists of three cartilaginous elements (Figs. 16C, 21) and an elongated barbed, terminal one that consists of a tissue other than calcified cartilage (Fig. 19). Of the calcified cartilage elements two proximal pieces are short and of rhombic outline (as preserved), and a third is a very long rod about $1\frac{1}{2}$ times the length of the braincase. The calcification of these elements consists of fine-grained “prisms” (Fig. 20) that give these structures a characteristic appearance on X-ray film. As preserved, all described pieces are flat, but in life they were no doubt more or less circular in cross section, surrounding a canal for the transmission of seminal fluid. The terminal element is preserved only in one specimen, PF13236, where it is not associated with the other pterygopodial structures (Fig. 8). However, its appearance on X-ray film matches terminal clasper elements observed, for example, in *Sibyrhynchus denisoni* (FMNH B83-961 and B83-811) from the Bethel Quarry, where these structures are preserved in situ. Along one side and near the end of this terminal clasper piece are three serrations

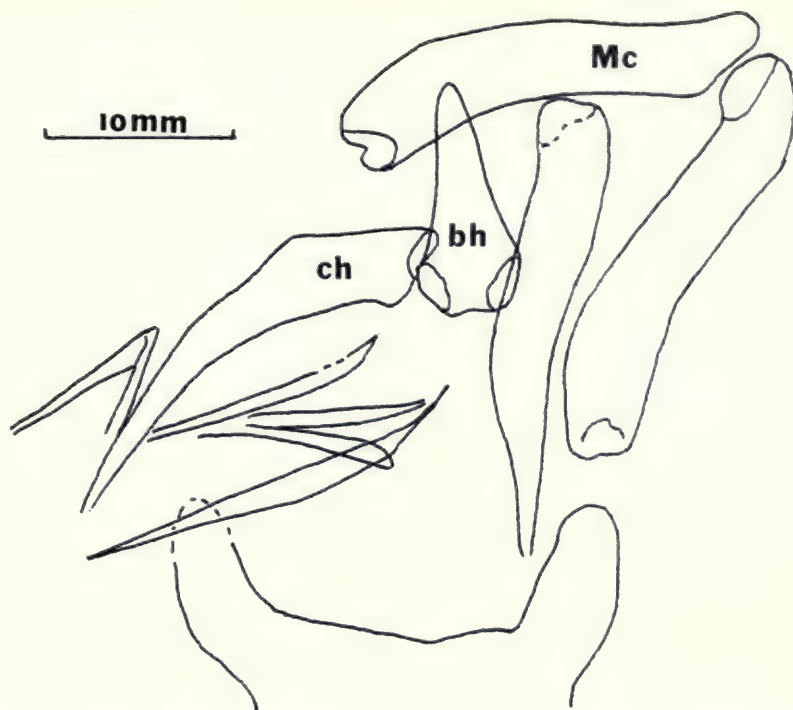


FIG. 13. Visceral cartilages of *Cervifurca nasuta*, PF6455, traced from an X-ray enlargement. bh, basihyal; ch, ceratohyal; Mc, Meckel's cartilage. At bottom front end of neurocranium.

or barbs (Fig. 19). This element is preserved in the form of a carbonaceous film. Because uncalcified cartilage is not preserved in the black shales containing this fauna, it may be assumed that the structure in question consisted of some other, perhaps ceratinous, tissue.

UNPAIRED FINS—The dorsal fin, located some distance behind the position of the pelvic fins, is preserved in situ in the concretion specimen UIMNH 11378 (Figs. 2, 3), and in disarticulated state in PF13228 (Fig. 15). In UIMNH 11378, the dorsal fin consists of eight radials that are pointed ventrally; dorsally they end abruptly, as if cut by shears. The radials of PF13228 have exactly the same shapes, suggesting that the dorsal tips remained uncalcified.

The tail fin is missing in all specimens available at present.

RECONSTRUCTION—The reconstruction drawings, Figure 21 in ventral view and Figure 22 in lateral view, are based on all available specimens, but of course primarily on the most completely preserved skeletons, and on UIMNH 11378. Overall, I believe, the drawings correctly represent the skeletal morphology of this animal, but because not every detail is actually documented in a spec-

imen (e.g., the placement of the tenacular hooks, or the exact number of radials in the pectoral fin), future revisions may well be required.

Discussion

The skeleton of *Cervifurca nasuta* conforms perfectly to the morphotype (*sensu* Kälin, 1945) of the family Iniopterygidae in that its jaw suspension is autodiastyltic—that is, the palatoquadrate is attached to the neurocranium by a joint (Stahl, 1980)—and the dentition teeth do not fuse to form tooth whorls across the jaws. The roof and floor of the mouth cavity are free of characteristically shaped armor plates, the products of fusion of large numbers of mucous membrane denticles, present in the members of the family Sibyrhynchidae, and in orimantal development perhaps seen in *Promexyele peyeri* among the Iniopterygidae. (Oriment, from *oriri* = to rise, is a term proposed by Othenio Abel (1914) for a structure in early phylogenetic development, in contrast to rudiment, which is consistently used in the

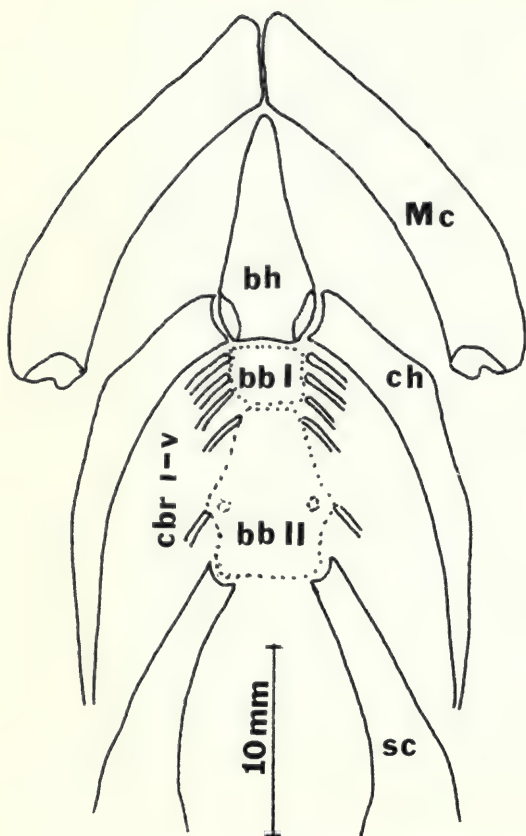


FIG. 14. Tentative reconstruction of ventral visceral elements. bb I and II, basibranchials I and II (not yet observed in this taxon); bh, basihyal; cbr I-V, ceratobranchials I-V; ch, ceratohyal; Mc, Meckel's cartilage; sc, scapulocoracoid.

German literature for a phylogenetically vanishing structure.)

Cervifurca nasuta differs, however, from all other presently known members of the order by its dorsoventrally flattened body shape, most strikingly apparent in the character of the brain-

case with orbits that suggest dorsolaterad-directed eyes, as in modern batoids; in all other species of iniopterygians where the skull is known, the orbits are roofed over by cartilage, thus restricting upward viewing. Also, a dorsoventral burial position occurs in every specimen where the neurocranium is preserved more or less intact. A batoid habitus is further suggested by the large pectoral fin web, modified pelvic fins that could hardly have been used in swimming, and the enormously enhanced pterygopodia. It may thus be concluded that *Cervifurca nasuta* was an inhabitant of the benthic realm (though probably not at great depth), a member of the mobile benthos.

DENTITION—The dentition as depicted in Figure 7C looks rather formidable. However, what is missing in that illustration are the soft tissues, the submucosa and the mucosa. In life these soft tissues covered the large tooth bases entirely, so that only the tooth crowns were visible and came into contact with prey. The largest diameters of the crowns, in the largest teeth, are only about 1 mm, and their length was not much greater. The dentition therefore, was not as impressive as Figure 7C would suggest, but it was no doubt quite effective in holding and piercing struggling prey.

The question arises: why the large tooth bases? In the two other genera of the family, the dentition teeth are minute in *Iniopteryx*, and are small, tricuspid denticles with small bases in *Promexylele*. In the Sibyrhynchidae, where the bases of entire tooth families are fused to form tooth whorls, the volume of the combined base may exceed many times that of the tooth crowns (Zangerl & Case 1973, Figs. 47i' and 47i'').

The tooth base serves, in chondrichthyans, to anchor the tooth by means of numerous collagen fiber bundles within the submucosa and the perichondrial membrane of the jaw skeleton. A large tooth base, therefore, affords a much firmer attachment of the tooth to the jaw than a small base.

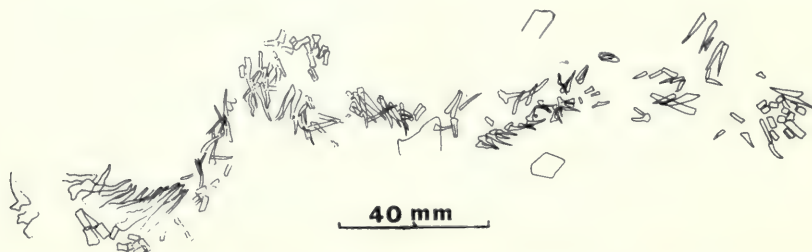


FIG. 15. Tracing of vertebral column of *Cervifurca nasuta*, PF13228 (XR: B83-996) from X-ray enlargement. Cervical vertebrae to the left. See also Figure 1.

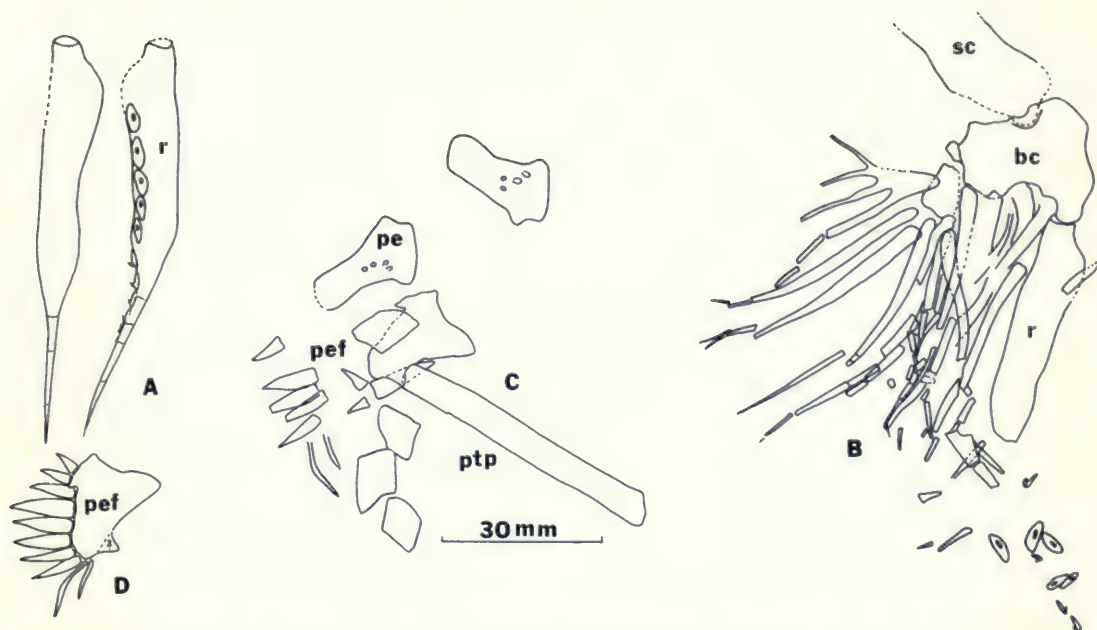


FIG. 16. X-ray shadow tracings, *Cervifurca nasuta*, PF13228 (XR: B83-996). A, Rasps with broken distal sections reassembled. B, Right pectoral fin as preserved. C, Pelvic area with one of the pelvic fins and proximal elements of one of the pterygopodia as preserved. D, Pelvic fin reassembled. bc, basal cartilage of pectoral fin; pe, pelvic cartilage; pef, pelvic fin; ptp, (part of) pterygopodium; r, rasp; sc, scapulocoracoid.

This, however, is not the whole explanation. Specimen PF13229 is about $\frac{4}{5}$ the size of PF13230, but the tooth bases of PF13229 are only about $\frac{1}{2}$ the diameter of those of PF13230, whereas the

basal diameters of the tooth crowns are about the same in both specimens. Because both sets of teeth appear to have been functional at the time of death, the tooth bases of the larger individual

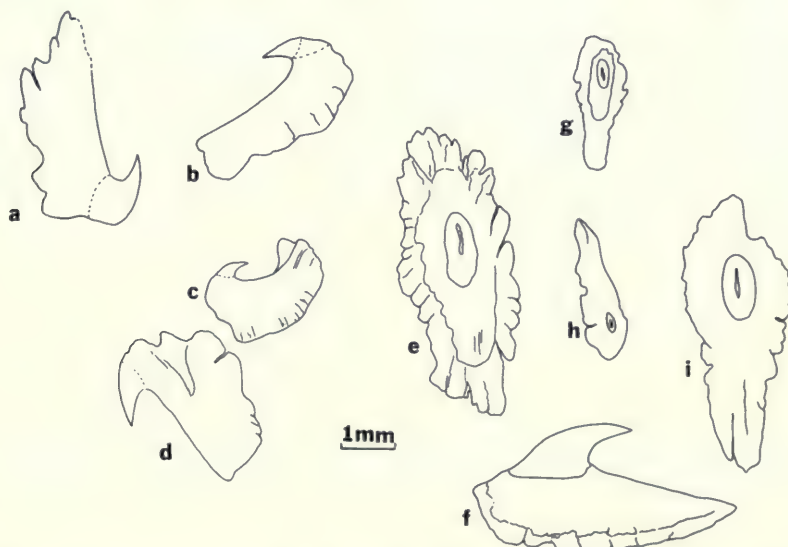


FIG. 17. Outline drawings of rasp and tenacular hooks of PF13230 (B83-135), showing variation in form and size. a-d, tenacular hooks; e-i, rasp hooks.



FIG. 18. Rasp and tenacular hooks rendered from specimens of *Cervifurca nasuta* with the aid of a Wild binocular microscope drawing tube. A, Large, proximal rasp hooks, PF13238 (B83-1039); B, C, large and small rasp hooks of PF13229 (B83-133C), one of them showing pulp cavity; D, tenacular hook of PF13238 (B83-1039); E, tenacular hooks of PF13229 (B83-133C).

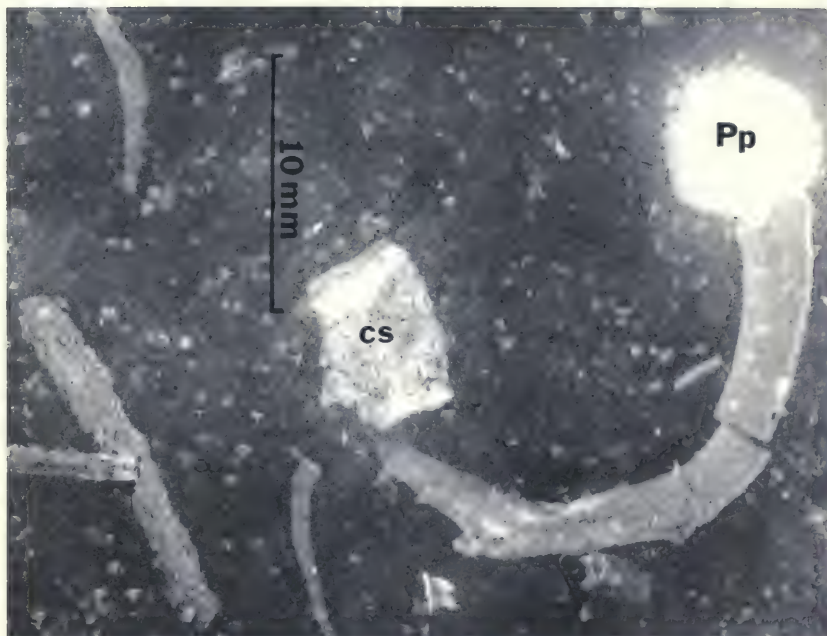


FIG. 19. X-ray negative enlargement of the terminal segment of the pterygopodium of *Cervifurca nasuta*, PF13236 (XR: B83-554), which does not consist of calcified cartilage. Shadows of unrelated structures: Pp, dermal denticle of *Petrodus patelliformis*; cs, ?pectoral fin cartilage, and below it near edge of picture, a compound dermal denticle of a caseodontid shark; in background miscellaneous debris and large numbers of tiny cladodont denticles (see caption of Fig. 1).

must have continued to grow to twice the diameter of those of the smaller specimen while in functional state.

This speaks for a rather slow rate of tooth replacement, even though the tooth crowns show no wear facets. These observations suggest that the large size of the tooth bases has little to do with requirements for strong attachment but is the result of continued sclerotization past the functional need for tooth stabilization. *Cervifurca nasuta* most likely preyed on soft-bodied invertebrates and immature fishes.

The above explanation of continued growth of tooth bases past the point of secure fastening of these structures to the substrate may apply as well to the specialized dermal denticles of the rasp and the tenacular hooks. These organs also have large bases, and those of the proximal rasp hooks, in particular, show finger-shaped projections both fore and aft, indicating continuing growth in both directions (Fig. 18).

PTERYGOPODIA—The pterygopodia of iniopterygians are structurally simple organs that consist of a variously jointed cylinder containing a lumen for the transmission of sperm. The segments con-

sist of a finely granular calcified cartilage, but in at least one species the terminal section is either sheathed in dentine or perhaps bone (*Iniopera richardsoni*), or consists of a substance other than cartilage, perhaps a ceratinous tissue (*Sibyrrhynchus denisoni*, *Cervifurca nasuta*, and three as yet undescribed sibyrrhynchids) that tends to be preserved as a carbonaceous film.

There are no characteristic familial or generic patterns to the pterygopodia; instead, the details of clasper organization, including the secondary sexual features, tenacular and rasp hooks, are typical for each species. The evolution of species-specific copulatory organs parallels a more common phenomenon in closely related insects, where it is thought to discourage or prevent hybridization.

NUMERICAL DISPARITY BETWEEN THE SEXES—As was pointed out earlier (p. 5), no female specimens of *Cervifurca* have been identified, and this is not solely due to the fact that partial and mutilated specimens lacking pterygopodia, rasp, and tenacular hooks cannot be recognized as females, let alone (if they also lack dentition teeth) as females of a particular species. The present collec-

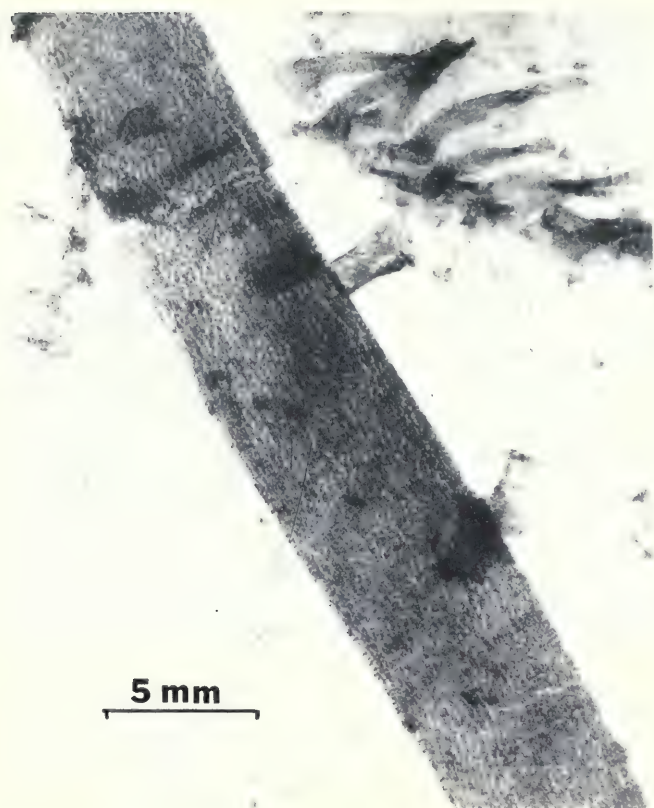


FIG. 20. X-ray positive enlargement of long pterygopodial segment of PF13228 (B83-996) to show the characteristic texture of the calcified cartilage "prisms" of these structures.

tions, indeed, contain very few adequately complete and well-preserved skeletons of iniopterygians that lack the mentioned characteristic male sex organs, and are hence unquestionable females. One such specimen (FMNH field no. B83-942) shows that the pelvic skeleton differs greatly, as should be expected, from those of males. Because adequately preserved female specimens are very rare it has not been possible, except in *Iniopteryx rushloui*, to assign them to described species.

The great numerical disparity between the sexes of all iniopterygian taxa in the present collections is real, rather than the result of our inability to recognize females among incomplete or poorly preserved specimens. The disparity existed in the burial environment that produced the black shales, and this raises the question why the females failed to be attracted to this unstable and no doubt hostile environment.

A discussion of this question requires a statement concerning the broader problems of where the fishes entombed in the black shales came

from. Zangerl and Richardson (1963) reached the conclusion that the burial environment could not have been the normal habitat of any of the fishes of the Mecca fauna, for reasons that are briefly summarized below.

There is much important evidence that the black carbonaceous Mecca and Logan Quarry shales, and similar shales at other stratigraphic levels, including the Excello Shale, were formed on freshly leveled coal-forest surfaces, shallowly inundated during marine transgressions. These marginal basin environments became covered by floating vegetation (flotants) that produced large quantities of black muds beneath them. Holm et al. (1969) published measurements of modern floatant productivity of more than 30 cm of organic mud per year beneath a floating mat of water hyacinth (*Eichhornia crassipes* (Mart.) Solms). The Pennsylvanian floatant (which probably was algal in composition) eliminated wave disturbance of the bottom mud, and the interstitial water of the mud was highly charged with hydrogen sulfide,

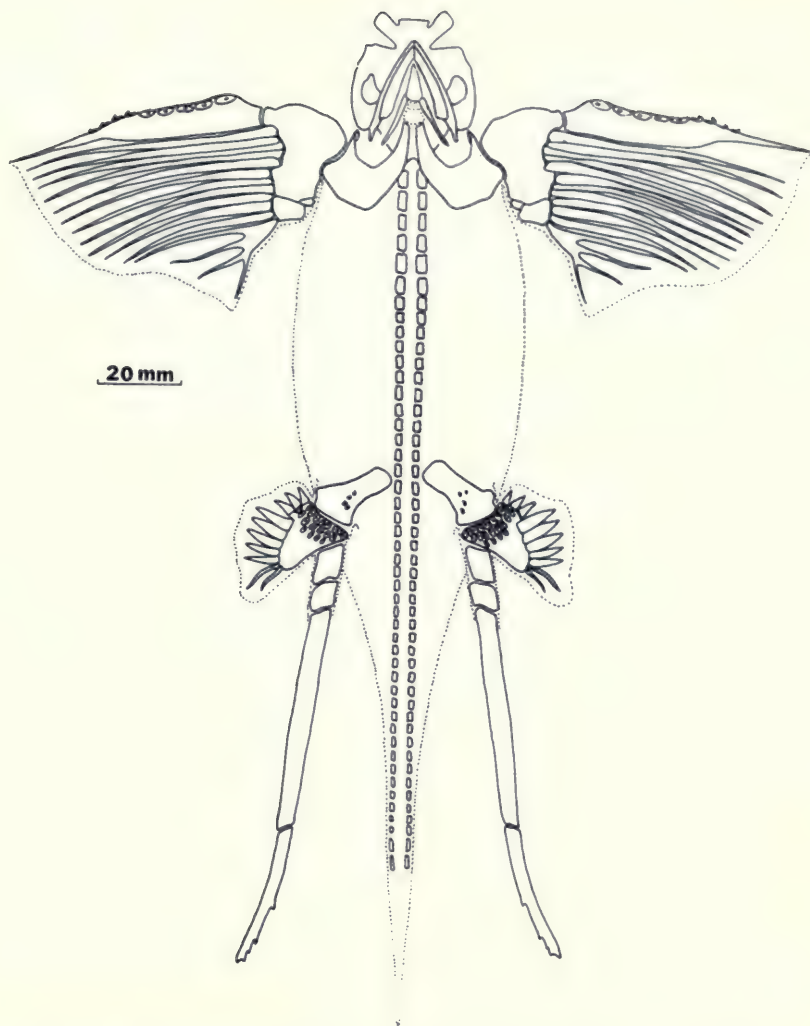


FIG. 21. Reconstruction of the skeleton of *Cervifurca nasuta*, in ventral view.

toxic to all forms of infauna, but an ideal environment for bacteria and other decomposers. Because of the unusually rapid deposition of organic debris, the mud environment was very favorable for the preservation of fish skeletons, including the calcified cartilage of chondrichthyans. For evidence supporting the above conditions and a detailed analysis of the paleoecological parameters of the black shales, see Zangerl and Richardson (1963); Coveney and Glascock (1989) corroborated many of the findings of Zangerl and Richardson using entirely different evidence.

Given the stated aspects of the black shale depositional environment, one must conclude that the animals entombed in the shales were not reg-

ular inhabitants of those environments, but rather were visitors from the deeper, more central parts of the basins that entered these marginal areas. There many, perhaps most, of the invaders became entrapped in residual ponds and succumbed to predation and injuries inflicted by predators (Zangerl & Richardson, 1963).

There is, however, some evidence that not all of the fishes preserved in the black shales were inhabitants of the epicontinental waters of the central North American basin complex. The presence of teeth of such sharks as *Cobelodus aculeatus* (Cope), *Stethacanthus altonensis* (St. John and Worthen), and *Phoebodus* sp. in the wash residues of central United States Pennsylvanian carbonates

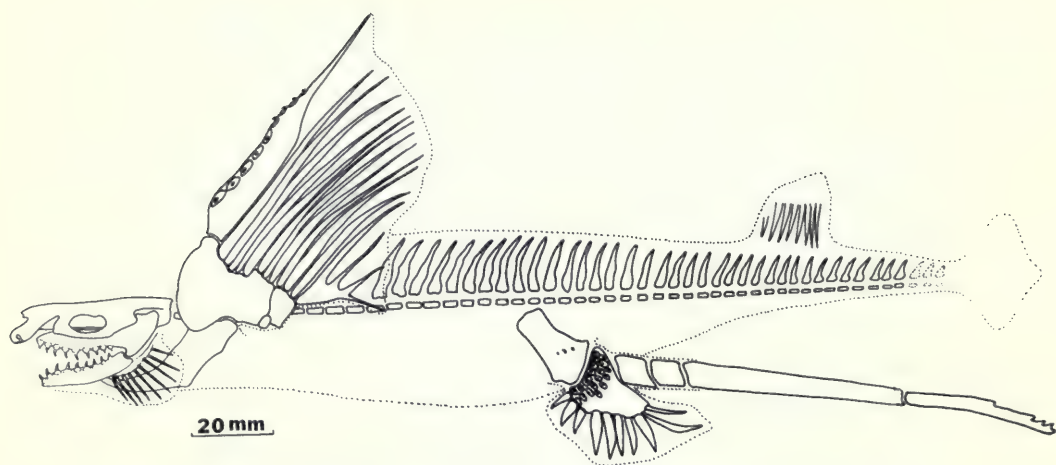


FIG. 22. Reconstruction of the skeleton of *Cervifurca nasuta*, in lateral aspect.

and drab shales suggests that these taxa inhabited the epicontinental marine basins and were widely distributed within them (Tway & Zidek, 1982, 1983a,b; Hansen, 1986). But remains of the most conspicuous and very abundant elements of the Mecca fauna, namely the iniopterygians, are missing in the mentioned wash residues.

The depositional history of the Pennsylvanian rock sequence of the structural Illinois basin, for example, includes numerous transgressions of marine waters over a large, shallow, subsiding epicontinental pan. These transgressions inundated and destroyed the coal forests that grew on the low and swampy lands adjacent to the deeper parts of the pan. The muds that accumulated on the former forest floor beneath mats of floating vegetation, and which have become the black carbonaceous shales, represent the initial consequences of some of the periodic transgressions.

It is thus entirely possible that the iniopterygians and some other cartilaginous fishes in the Mecca fauna (e.g., the caseodontoid and edestoid eugeneodontids) entered the epicontinental waters from deeper, oceanic realms during episodes of transgressive inundation, and were not denizens of the shallow basin provinces, but were members of the oceanic fish community of that time.

Smith et al. (1994) compiled a most interesting set of 31 paleogeographic maps of the world from the Pliocene back to the Early Triassic showing the changing configuration of the land masses and the paleocoastlines. The Early Triassic map shows Pangaea with North America plus Greenland tightly joined to Africa and South America, which, in the aftermath of a major (Permian) gla-

ciation, means that the landmasses stood high relative to mean sea level. In Pennsylvanian (e.g., Desmoinesian) time, by contrast, marine waters transgressed repeatedly over much of the lower North American continental area. Wanless (1969) suggested that two belts of transgression originated from an area in southern California or northwestern Mexico. One arm extended up to Montana and from there to the Midwest; the other reached eastward south of the Ozark uplift to the Appalachian basins. However, the elevation of the Ouachita deformed belt blocked the eastern part of this seaway, so that Desmoinesian and later transgressions had to spread north on the west side of the Ozarks to reach the Illinois basin, for example.

If my interpretation of the iniopterygians and some of the elasmobranchs of the Mecca fauna as denizens of oceanic waters is correct, these fishes would have had to travel some 3,000 km or more to reach the Illinois basin. More likely seems to be the existence of an oceanic geosyncline (perhaps alluded to by Wanless [1969, Fig. 1] under the name of Possible Gulf of Mexico Basin) from which by Desmoinesian time transgressions might have surged northward.

Under this interpretation, the Mecca fish fauna would represent a mixture of basin elements and truly oceanic ones, a matter of considerable interest, because the Carboniferous record of oceanic chondrichthyans is rather meager indeed.

Of the oceanic chondrichthyan fish community, the Mecca fauna appears to have sampled both open water endurance swimmers (e.g., *Caseodus* and relatives) with large forked tail fins at least

as stiff as those of Recent swordfish, as well as the iniopterygians, forms that perhaps inhabited the shelf areas of an oceanic seaway.

Extensive collecting at many black shale outcrops in Parke, Vermillion, Fountain, Vigo, and Pike counties, and four quarries in Parke and Pike counties has shown that the various taxa of the Mecca fish fauna are not represented in equal proportions everywhere; rather, in each locality one or more taxa are common, whereas the rest are rare or absent. This phenomenon probably reflects the geographically uneven distribution of the fishes immediately prior to and during the transgressions, when many of them entered the floatant environments.

Returning to the question of the great rarity of female iniopterygians, and also of females of the elasmobranch *Danaea meccaensis* (Williams, 1985) we can exclude, in the case of the iniopterygians, the possibility of preferential predation affecting the unarmored females, because all the male specimens represent individuals that died of the effects of predator-inflicted injuries. In *Danaea* neither sex has any kind of armature. The uneven representation of the sexes perhaps merely indicates that the females preferred the deeper and presumably clearer waters of the more central parts of the basins, shunning whatever inducements the dark, shallow, and treacherous floatant environments offered to some 38 species of chondrichthyans now preserved in the black shales that resulted from those rich organic mud accumulations.

Conclusions

The present account introduces a new genus of iniopterygian, *Cervifurca nasuta*, with a somewhat dorsoventrally flattened body and eyes that faced dorsolaterad, very large pectoral fins, a peculiarly modified pelvic fin skeleton of uncertain function, and enormously enhanced pterygopodia. This new form enlarges our knowledge of the adaptive radiation of the Iniopterygia, which, along with some sharks, most likely were not part of the fish fauna of the epicontinental basin complex of North America but may have ventured, with repeated transgressions of oceanic waters, into the shallow basins with their marginal floatant environments.

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